International Institute for Applied Systems Analysis
IIASA www.iiasa.ac.at

On the interplay of environmental changes and fishing pressure in exploited fish stocks

Boukal, D.S., de Roos, A.M., Persson, L. and Heino, M.

IIASA Interim Report
July 2010

International Institute for
Applied Systems Analysis
Schlossplatz 1
A-2361 Laxenburg, Austria

Tel: +43 2236 807 342
Fax: +43 2236 71313
E-mail: publications@iiasa.ac.at
Web: www.iiasa.ac.at

Interim Report **IR-10-023**

On the interplay of environmental changes and fishing pressure in exploited fish stocks

David S. Boukal (boukal@entu.cas.cz)
André M. de Roos (a.m.deroos@uva.nl)
Lennart Persson (lennart.persson@emg.umu.se)
Mikko Heino (mikko.heino@imr.no)

Approved by

Ulf Dieckmann
Leader, Evolution and Ecology Program

July 2011

Theme session: ICES CM 2010/M:15

On the interplay of environmental changes and fishing pressure in exploited fish stocks

David S. Boukal[1,⋆], **Andre M. de Roos**[2], **Lennart Persson**[3] **and Mikko Heino**[4,5,6]

[1] Biology Centre AS CR, Branisovska 31, CZ-37005 Ceske Budejovice, Czech Republic
[2] Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, PB 94084, NL-1090 GB Amsterdam, The Netherlands
[3] Department of Ecology and Environmental Science, Umeå University, SE-90187 Umeå, Sweden
[4] Institute of Marine Research, Postboks 1870 Nordnes, N-5817 Bergen, Norway
[5] Department of Biology, University of Bergen, Bergen, Norway
[6] International Institute for Applied Systems Analysis, Laxenburg, Austria
⋆ corresponding author

e-mail addresses: boukal@entu.cas.cz, a.m.deroos@uva.nl, lennart.persson@eg.umu.se, mikko.heino@imr.no

Keywords: life history evolution, stochasticity, harvesting, population dynamics, density dependence, fisheries.

Abstract

Fish in many exploited stocks grow faster and mature earlier at either larger or smaller sizes in comparison to pre-exploitation periods. These changes can be driven by both genetic and phenotypic responses. At the same time, these stocks may adjust to other changes of the environment such as increasing/decreasing overall productivity or changes in temperature. Using a model of planktivorous fish with annual spawning and size- and density-dependent individual growth, we ask if the interplay of environmental change and fishing pressure could lead to stabilizing, disruptive or directional selection on age and size at maturation in the stock. This question is particularly relevant for habitats exposed to significant directional change in the environment, the prime example being many man-made inland reservoirs.

Introduction

Fish in exploited stocks typically exhibit faster growth. This change is associated with earlier maturation, often at smaller sizes. Such phenotypic life history changes can result from both genetic and plastic responses (Law 2000, Hutchings 2005, Jørgensen et al. 2007). The most common plastic response is due to ecological feedback: decreased competition allows for compensatory growth and thus earlier maturation if individuals mature around a fixed threshold size (Engelhard and Heino 2004). Moreover, empirical studies and life-history theory predicts that size-specific or indiscriminate harvesting selects for early maturation at small size (Roff 2002, Jørgensen et al. 2007) and this change may become irreversible if the fish exhibit alternative, evolutionary and ecologically stable life histories with early and late maturation (de Roos et al. 2006).

However, life history models dealing with fisheries-induced evolution typically assume environmental drivers that do not change over time. We have therefore only limited understanding how could environmental trends, occurring over realtive short timescales, such as fluctuations in climate or changes at basal trophic levels, change selection gradients and possibly alter life histories of the focal fish stock. These considerations are particularly important for freshwater lakes and man-made reservoirs. Fish in these water bodies are often under considerable fishing pressure and, at the same time, their natural environment is undergoing significant changes on decadal or even annual timescales (Edeline et al. 2007). In this paper we focus on several drivers that can affect fish life histories both directly, e.g. by the lengthening or shortening of growth season, and indirectly through density-dependent feedback, e.g. by affecting the amount and quality of food resources. We ask if such environmental trends alone could lead to changes in selection gradient on size at maturation, thereby shifting evolutionary optima over time. Moreover, we examine if the potential changes in evolutionarily stable size at maturation might mitigate fisheries-induced evolution.

Methods

We use a well-studied size-structured population dynamical model to describe the population dynamics of the fish stock (Persson et al. 1998, de Roos and Persson 2001). The equations and parameter values describing the individual life history are based on roach, a well-studied planktivorous freshwater fish (Tables 1 and 2). The population-level equations were summarized in de Roos et al. (2006) and Boukal et al. (2006). The model assumes seasonality in reproduction but no external seasonal input (e.g. fluctuations in temperature). New cohorts recruit to the juvenile and adult population at age 1 and the length of 50 mm with maximum juvenile condition. Young-of-the-year fish do not feed on the common resource, which follows a semi-chemostat dynamics and is shared by all fish older than 1 year. We assume that the number of recruits follows a Ricker-type stock-recruitment relationship corrected for the spawning stock condition, being equal to $R_A E \exp(-2 \cdot 10^{-9} E)$, where E is the total number of eggs spawned the year before recruitment and R_A is the survival probability to age 1 when few eggs are spawned. Following Boukal et al. (2006) we incorporate limited environmental stochasticity in recruitment and survival of recruited fish directly into the model. We assume that recruitment is random with $R_A \sim N(0.01, 0.001)$ and for the sake of computational simplicity, we assume that the background mortality rate $\mu_b \sim LogN(\log(0.014), 0.02)$ is constant within each year. The resulting stochasticity in individual survival indirectly feeds back via the resource and thus leads to stochastic growth rates, differing between age cohorts.

For the parameter values used here, two alternative life histories are both ecologically and evolutionary stable (de Roos et al. 2006, Boukal et al. 2006). They represent an 'early' phenotype which, in the absence of stochasticity, matures during the second year at only 69 mm length, and a 'late' phenotype

which matures only during the third year at 101 mm. The 'late' phenotype is consistently larger at any given age and consequently has higher reproductive output at each reproductive event. We also assume that individuals maturing at large size have a competitive advantage due to positive correlation between L_{mat} and maximum feeding rate A_{max}. This assumption embodies a mechanism which can oppose selection pressures towards maturation at small size; see suggestions in Munch et al. (2006) for other possible correlations. Both phenotypes are evolutionary stable because they optimize the within-season timing of the onset of maturation (Kozlowski 1996). Unharvested populations of both early- and late-maturing phenotype settle near an ecological equilibrium with minor fluctuations in resource and fish stock size due to seasonality and environmental stochasticity.

To examine the evolution of size at maturation of both harvested and unharvested stock under environmental change, we use the quantitative genetics approach developed in de Roos et al. (2006). We represent genetic variability in the consumer population as follows. Individuals born within the same year are assumed to group into a number of different subcohorts, which are identical at birth, but differ in maturation size L_{mat}. Consumers within the same sub-cohort are identical. We use 11 such sub-cohorts, each with its own phenotype: one with the new mean $L^{\star}_{mat}$ value, five with lower and five with higher L_{mat} values, equidistantly separated by a factor of $L^{\star}_{mat}\sigma_p/2$ with $\sigma_p = 0.10$. Newborn individuals are distributed over the subcohorts to reflect a discrete approximation to the normal distribution. Selection differential S is calculated using standard techniques, equating individual fitness with the number of eggs spawned; in each reproductive event, S equals the difference between the mean L_{mat} weighed by cohort fecundity and mean L_{mat} in all 1+ year old fish. We constrain the change in L_{mat} between the parent and offspring generation as $\Delta(L_{mat}) = \min(h^2 S, L^{\star}_{mat}\sigma_p/2)$ to keep the phenotypic distribution approximately normal, and assume constant heritability $h^2 = 0.3$.

We consider five possible types of environmental change. Each type is characterized by one varying environmental parameter: resource carrying capacity K, resource growth rate r, optimal foraging size w_0, maximum survival probability for recruits R_A and growth season duration Y. We explore four different levels of environmental change for each of these parameters: fast decline, slow decline, slow increase and fast increase. More specifically, we first allow the population to reach an ecological and evolutionary equilibrium with the set of parameters given in Table 1. We subsequently change the varying environmental parameter linearly over 50 years from the baseline value given in Table 1 to a value that is 25% lower (fast decrease), 5% lower (slow decrease), 5% higher (slow increase) or 25% higher (fast increase) and then keep it at that level for another 50 years.

In addition to the environmental change, we assume that the fish stock may or may not beharvested during the 50-year period in which the environmental parameter changes from the baseline to the final value. We model harvesting as in de Roos et al. (2006). Probability of being harvested increases sigmoidally with body size and is characterized by the harvesting size threshold h_0, at which harvesting reaches half its maximum value, and harvesting intensity h_{max}, i.e. the annual harvesting mortality for individuals well above the threshold. Each year prior to reproduction and recruitment, we harvest a fraction $h_{max}/(1 + \exp(0.15(h_0 - l))$ of each size class l of recruited fish. For each scenario, we record changes in age and size at maturation and compare them to the evolutionary (pseudo)equilibrium achieved before the period of exploitation and environmental change.

Results

Impact of changing environment on age and size at maturation: unharvested populations

In the absence of fishing, both 'late' and 'early' phenotypes are evolutionary stable for almost all types of environmental change. Changing resource carrying capacity and growth rate and changing optimal for-

aging size have the lowest relative impact on size at maturation, as the fast changes lead only to 1–1.5% changes in the average value of evolutionarily stable size at maturation for both phenotypes. Increasing survival of recruits leads to decreasing L_{mat}; that is, its effect is opposite to that of icreasing resource carrying capacity, growth rate or optimum foraging size, which all result in increasing L_{mat}. Moreover, the magnitude of the relative impact of recruit survival is about twice as large as the effect of the previous three environmental parameters: fast decrease in recruit survival leads to about 3% decrease in L_{mat} and fast increase to about 3% increase in L_{mat} (Table 3 and 4). The relative impacts of slow changes of all four parameters are qualitatively similar but, as one would expect, much smaller in magnitude.

On the other hand, the impact of changing season length Y on the 'late' phenotype is stronger and qualitatively different (Table 3). The slow decrease in season length leads to maturation at approximately 3% smaller size, and an increase of similar magnitude in size at maturation arises when season length slowly increases. The changes in size at maturation are even higher for the rapidly changing season length but, surprisingly, both the increase and decrease in season length lead to a decline in size at maturation for the late-maturing phenotype. This is because the phenotype with larger L_{mat} begins to mature already during the second year as the season becomes longer, and consequently both the late-maturing and early-maturing phenotype converge towards a joint evolutionarily endpoint.

Impact of changing environment on age and size at maturation: harvested populations

Possible qualitative evolutionary outcomes of harvesting depend both on the harvesting mortality and harvesting threshold. The changes of age and size at maturation qualitatively follow earlier results for deterministic and stochastic dynamics (compare de Roos et al. (2006) and Boukal et al. (2006)). Onset/cessation of harvesting first triggers a fast plastic response in age at maturation followed by a gradual evolutionary response in size at maturation.

We mention here only results for harvesting threshold $h_0 = 100$ mm and harvesting mortality $h_{max} = 0.6$. This harvesting regime induces a rapid evolution of the 'late' phenotype towards the 'early' phenotype, i.e. towards maturation during the second year at ca. 70 mm length (de Roos et al. 2006, Boukal et al. 2006).

When the stock is exposed simultaneously to fishing mortality and environmental change, we find that the latter usually contributes relatively little to fisheries-induced evolution (Table 3 and 4). This main result therefore agrees well with the minor impact of environment on life histories documented in the previous secion. Nevertheless, the contribution of environmental change is often far from obvious. First, the rate at which the 'late' phenotype evolves towards the 'early' phenotype increases with higher resource productivity (increasing K or r); on the other hand, increasing optimal foraging size slows down that rate. Second, we have identified at least two scenarios in which the environmental change might work against fisheries-induced evolution. Although size at maturation of the 'late' phenotype always declines during the time interval of 100 years considered in our simulations, the corresponding age at maturation remains close to or above 2 years for scenarios characterized by increasing optimum foraging size and increasing survival of the recruits. In these two scenarios, growth is slowed down because of less efficient foraging at smaller sizes or because of tighter density dependence due to improved survival. As a consequence, even small fish can still mature during their third year; we have shown earlier that this condition is a prerequisite for an evolutionary reversal back to late maturation at larger size (de Roos et al. 2006).

Conclusions

Our results suggest that changing environmental conditions predominately lead to only minor changes in evolutionarily stable age and size at maturation. We predict that even under rather pessimistic scenarios of fast environmental change (change of environmental parameter by 25% of its initial value within 50 years, followed by 50 years in the newly established environment) the evolutionarily stable size at maturation changes by at most a few percent. This result is encouraging, as many inland freshwater reservoirs undergo the process of intensive eutrophication from sewage and fertilizers used in agricultural production or, perhaps less frequently, become much less productive due to the onset of wastewater treatment (V. Hejzlar, pers. comm.). It seems that in our examples, most of the environmental change is absorbed by population-level regulatory mechanisms which leave little room for subsequent changes at the level of individual life histories. The major exception from this observation occurred for season length: we have showed that while slowly increasing season length might preserve both the late- and early-maturing phenotype over longer timescales, rapidly increasing season length will lead to the demise of the late-maturing phenotype. Instead of growing even larger and maturing still in the third year, individuals of this phenotype will begin to mature already during their second year of life and their life history charactristics will gradually merge with those of the early-maturing phenotype. We thus conclude that rapid environmental change towards higher spring/summer temperatures and subsequently longer growing seasons might lead to the loss of life history diversity at the expense of 'slow' life history strategies.

On the other hand, environmental change might occassionally serve as a buffer against detrimental life history changes brought about by fishing pressure. Favourable changes in the environment might thereby prolong the time window available for implementation of management actions aimed at mitigating the evolutionary consequences of fishing. We have identified at least two such pussible buffers: increased survival of recruits and increased optimal attack size. Recruits might survive better under a variety of plausible circumstances (removal of predators, milder winters, improved feeding conditions for young-of-the-year fish). Optimal attack size might increase when the resource, treated as a homogeneous quantity in this study, changes its properties such that larger fish become more efficient at feeding. In planktivorous fish, this might occur for example when plankton community shifts towards larger body sizes.

Acknowledgements

The work of D.S.B. and M. Heino on this study is supported by the subproject 'Monitoring the environment of man-made lakes: what can fisheries data and models tell us?' (reg. no. A/CZ0046/2/0029) supported from the EEA/Norway grants and the Czech Republic state budget by means of the Research Support Fund.

References

Boukal, D. S., A. M. de Roos and L. Persson. 2006. How does stochasticity affect evolutionary regime shifts in age and size at maturation? ICES CM 2006/H:05.

de Roos, A. M. and L. Persson. 2001. Physiologically structured models - from versatile technique to ecological theory. Oikos 94:51–71.

de Roos, A. M., D. S. Boukal and L. Persson. 2006. Evolutionary regime shifts in age and size at maturation in exploited fish stocks. Proceedings of the Royal Society London B 1596:1873–1880.

Edeline, E., S. M. Carlson and L. C. Stige. 2007. Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection. Proceedings of the National Academy of Sciences 104:15799–15804.

Engelhard, G. H. and M. Heino. 2004. Maturity changes in Norwegian spring-spawning herring *Clupea harrengus*: compensatory or evolutionary responses? Marine Ecology Progress Series 272:245–256.

Hutchings, J. A. 2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 62:824–832.

Jørgensen, C., K. Enberg, E. S. Dunlop, R. Arlinghaus, D. S. Boukal, K. Brander, B. Ernande, A. Gårdmark, F. Johnston, S. Matsumura, H. Pardoe, K. Raab, A. Silva, A. Vainikka, U. Dieckmann, M. Heino and A. D. Rijnsdorp. 2007. Managing evolving fish stocks. Science 318:1247–1248.

Kozlowski, J. 1996. Optimal allocation of resources explains interspecific life-history patterns in animals with indeterminate growth. Proceedings of the Royal Society London B 263:559–566.

Law, R. 2000. Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science 57:659–668.

Munch, M. R., S. B. Munch, S. Chiba and D. O. Conover. 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. Ecology Letters 9:142–148.

Persson, L., K. Leonardsson, A. M. de Roos, M. Gyllenberg and B. Christiansen. 1998. Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. Theoretical Population Biology 54:270–293.

Roff, D. A. 2002. Life history evolution. Sinauer Associates, Sunderland, Massachusets.

subject	**symbol**	**value**	**unit**	**interpretation**
Consumer	N	-	$\#$	cohort size
	x	-	g	irreversible mass
	y	-	g	reversible mass
Growth season	Y	90	day	length of year
Resource	R	-	g L^{-1}	resource density
	r	0.1	d^{-1}	population growth rate
	K	0.003	g L^{-1}	carrying capacity
	V	10^9	L	lake volume
Ontogeny	w_b	1.4×10^{-3}	g	total egg mass
	l_{exp}	0.29	-	allometric exponent
	l_c	50.2	mm $g^{-l_{exp}}$	allometric scalar
	L_{mat}	evolving	mm	maturation size (body length)
	q_j	0.74	-	juvenile max. condition
	q_a	1.0	-	adult max. condition
	k_r	0.5	-	gonad-egg conversion efficiency
Planktivory	α	1.0	-	allometric exponent
	A_{max}	1.0×10^5	L d^{-1}	max attack rate
	w_o	50.0	g	optimal foraging size (standardized mass)
Handling	ξ_1	6.0	d $g^{-(1+\xi_2)}$	allometric scalar
	ξ_2	-0.81	-	allometric exponent
Metabolism	ρ_1	0.033	$g^{(1-\rho_2)}d^{-1}$	allometric scalar
	ρ_2	0.77	-	allometric exponent
	k_e	0.61	-	conversion coefficient
Mortality	μ_0	0.014	d^{-1}	background mortality rate
	q_s	0.2	-	starvation condition threshold
	s	0.2	d^{-1}	starvation rate coefficient

Table 1: Variables and model parameters. All parameters except Y, R, r, K and V refer to individual-level processes; values for Y, r, K and w_0 are baseline values (see text). All values are based on a well-studied freshwater system involving a planktivorous fish and zooplankton (de Roos and Persson, 2001).

Subject	**Equation**
Standardized mass	$w(x) = (1+q_j)x$
Body length	$L(x) = l_c(w(x))^{l_{exp}}$
Attack rate	$A(x) = A_{max}\left(\frac{w(x)}{w_o}\, e^{\left(1-\frac{w(x)}{w_o}\right)}\right)^{\alpha}$
Handling time	$H(x) = \xi_1\, w(x)^{\xi_2}$
Food intake rate	$I(x) = \dfrac{A(x)R}{1+H(x)A(x)R}$
Assimilated energy	$E_a(x) = k_e I(x)$
Maintenance requirements	$E_m(x,y) = \rho_1(x+y)^{\rho_2}$
Energy balance	$E_g(x,y) = E_a(x) - E_m(x,y)$
Fraction of energy allocated to growth in irreversible mass	$\kappa(x,y) = \begin{cases} \dfrac{y}{(1+q_j)q_j x} & \text{if } L(x) \le L_{mat} \text{ and } E_g > 0 \\ \dfrac{y}{(1+q_a)q_a x} & \text{if } L(x) > L_{mat} \text{ and } E_g > 0 \\ 0 & \text{otherwise} \end{cases}$
Starvation mortality	$\mu_s(x,y) = \begin{cases} s\left(q_s\dfrac{x}{y} - 1\right) & \text{if } y < q_s x \\ 0 & \text{otherwise} \end{cases}$
Total mortality	$\mu(x,y) = \mu_0 + \mu_s(x,y)$
Fecundity	$F(x,y) = \begin{cases} k_r\,(y - q_j x)/w_b & \text{if } L(x) > L_{mat} \text{ and } y > q_j x \\ 0 & \text{otherwise} \end{cases}$

Table 2: Individual-level equations used in the simulations, see also de Roos and Persson (2001), de Roos *et al.* (2006) and Boukal *et al.* (2006).

trending parameter	**direction**	**harvesting**	L_{mat} (mm)	A_{mat} (years)
none	–	no	101.2 ± 0.17	2.51 ± 0.07
K	-0.5	no	99.7 ± 0.18	2.53 ± 0.06
	+0.5	no	102.6 ± 0.14	2.48 ± 0.06
r	-0.5	no	99.7 ± 0.18	2.53 ± 0.06
	+0.5	no	102.5 ± 0.14	2.48 ± 0.06
w_0	-0.5	no	99.6 ± 0.08	2.37 ± 0.07
	+0.5	no	101.7 ± 0.20	2.58 ± 0.06
R_A	-0.5	no	104.5 ± 0.07	2.35 ± 0.08
	+0.5	no	96.9 ± 0.17	2.57 ± 0.05
Y	-0.1	no	98.0 ± 0.18	2.55 ± 0.07
	+0.1	no	103.6 ± 0.13	2.44 ± 0.06
	-0.5	no	92.2 ± 0.17	2.85 ± 0.04
	+0.5*	no	89.1 ± 0.45	1.87 ± 0.02
none	–	yes	76.8 ± 0.23	1.88 ± 0.02
K	-0.5	yes	78.0 ± 0.40	1.93 ± 0.03
	+0.5	yes	$75.6 \pm 0.0.05$	1.84 ± 0.02
r	-0.5	yes	78.0 ± 0.41	1.93 ± 0.03
	+0.5	yes	75.9 ± 0.31	1.84 ± 0.02
w_0	-0.5	yes	73.2 ± 0.20	1.80 ± 0.03
	+0.5**	yes	80.8 ± 0.49	1.99 ± 0.04
R_A	-0.5	yes	76.7 ± 0.37	1.80 ± 0.03
	+0.5**	yes	80.9 ± 0.40	2.08 ± 0.05
Y	-0.5	yes	80.8 ± 0.34	1.78 ± 0.03
	+0.5	yes	89.1 ± 0.45	1.87 ± 0.02

Table 3: Summary of main results for the 'late' phenotype. Direction = fraction by which the trending parameter changes over the first 50 years (see text for details); harvesting ($h_0 = 100$m, $h_{max} = 0.6$) implemented only during the first 50 years. L_{mat} and A_{mat} given as mean$\pm$S.D. of the values at the end of the 100-year simulation. * = evolutionary regime shift to earlier maturation at smaller size; ** = (likely) cases of prevented evolutionary regime shifts. All results based on $n = 10$ replicates; results of slow environmental change shown only for season length Y in the absence of harvesting.

trending parameter	**direction**	**harvesting**	L_{mat} (mm)	A_{mat} (years)
none	–	no	68.8 ± 0.05	1.74 ± 0.03
K	-0.5	no	68.0 ± 0.04	1.75 ± 0.04
	+0.5	no	69.8 ± 0.05	1.73 ± 0.03
r	-0.5	no	68.0 ± 0.04	1.75 ± 0.04
	+0.5	no	69.8 ± 0.05	1.73 ± 0.03
w_0	-0.5	no	68.5 ± 0.06	1.71 ± 0.03
	+0.5	no	69.3 ± 0.04	1.76 ± 0.03
R_A	-0.5	no	71.4 ± 0.07	1.71 ± 0.04
	+0.5	no	67.1 ± 0.03	1.76 ± 0.03
Y	-0.5	no	66.7 ± 0.13	1.84 ± 0.03
	+0.5	no	74.2 ± 0.09	1.68 ± 0.02
none	–	yes	67.9 ± 0.05	1.72 ± 0.03
K	-0.5	yes	67.3 ± 0.04	1.73 ± 0.03
	+0.5	yes	68.8 ± 0.05	1.71 ± 0.04
r	-0.5	yes	67.3 ± 0.04	1.73 ± 0.03
	+0.5	yes	68.8 ± 0.05	1.71 ± 0.04
w_0	-0.5	yes	67.7 ± 0.05	1.69 ± 0.04
	+0.5	yes	68.4 ± 0.04	1.75 ± 0.03
R_A	-0.5	yes	69.6 ± 0.13	1.67 ± 0.04
	+0.5	yes	66.3 ± 0.04	1.73 ± 0.04
Y	-0.5	yes	70.5 ± 0.20	1.61 ± 0.02
	+0.5	yes	74.2 ± 0.09	1.68 ± 0.02

Table 4: Summary of main results for the 'early' phenotype. Direction = fraction by which the trending parameter changes over the first 50 years (see text for details); harvesting ($h_0 = 100$m, $h_{max} = 0.6$) implemented only during the first 50 years. L_{mat} and A_{mat} given as mean$\pm$S.D. of the values at the end of the 100-year simulation. All results based on $n =$10 replicates.